

(8) As a general rule the entrance of the azygos vein or veins into the precaval or precavals is more anterior in position in Mammals, occupying a lower position in the series than in more specialised types, *i. e.* opposite to second rib instead of fifth or sixth. This corresponds with ontogenetic shifting back of heart and blood-vessels.

(9) The conditions observable in the newly-born young of *Myopotamus coypu* seem to show that the postcardinals may persist as such at least up to the time of birth, and in some adult Rodents one is also persistent.

(10) The same species shows that the azygos of the adult is independent—except for a very short tract at its opening into the precava—of the postcardinal of its side, thus confirming the embryological results of others who have affirmed that only the very commencement of the azygos is traceable to the persistent postcardinal of its side.

(11) It is probable that the veins called “azygos” in adult Mammals are not in every case strictly homologous veins. Where there is but one azygos present (*e. g.* Carnivora) it is probable that that vein is the true azygos, except in the abdominal region where it is formed by the persistent postcardinal. In cases where there are two azygos veins both may be (? certain Marsupials) persistent postcardinals, or one of the two may be a remnant of the postcardinal, the other being a true azygos.

(12) These and some other facts and conclusions lead to the inference that the true azygos vein of Mammals (*i. e.* that formed by an outgrowth of the postcardinal) is a structure which has been developed in the Eutheria.

## 5. Ideas on the Origin of Flight.

By Dr. Baron FRANCIS NOPCSA.

[Received February 8, 1907.]

(Text-figures 74–82.)

Although much has been written on the origin of flight, yet till now no really satisfactory explanation for this kind of locomotion has been found. This is, so far as I can understand, mainly due to the fact that it has on *à priori* grounds been supposed that all the principal groups of flying vertebrates—namely, Pterosaurs, Bats, and Birds—originated in a similar manner, without fully appreciating the fundamental fact that, from the mechanical standpoint, patagium and feather are two perfectly different organs.

A patagium is a soft flexible membrane and in consequence requires, to be effective, numerous firm radial supports originating from the body that has to be carried, whereas for a series of semirigid but elastic quills one line of attachment is sufficient.

In consequence of this difference, a patagium-flyer must always

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adapt fore and hind limbs and tail to the support of the patagium, whereas in a generalised feathered animal only the feather-supporting elements need become affected by violent specialisation. The development of the posterior limb in such an animal is but little, if at all, affected by the development of flight (foot in Eagle, Parrot, Woodpecker, Nightingale, Goose, Stork, Ostrich, &c.).

As to flight itself we have to distinguish, as partially already pointed out by Dollo, three distinct stages of evolution: first parachute or *passive flight*, then flight by flapping the wings or *flight by force*, and lastly soaring or *flight by skill*.

As Langley and Lucas pointed out in their highly interesting papers, the soaring birds lack carrying power (in accordance with which fact the *crista sterni* is often comparatively feebly developed), while flight by flapping of the wings, as shown by the generally soaring Eagle when carrying prey, enables the animal to support a good deal of weight.

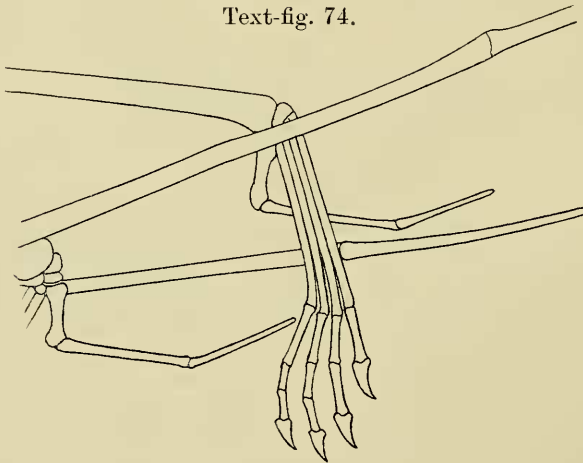
That soaring birds show a sharply pointed wing, while birds that fly mainly by flapping display a wing with a more or less rounded outline, is well known.

After these preliminary, but I think essential, observations, I shall now point out some characters of Pterosaurs, flying Mammals, Dinosaurs, and Birds that have not yet been brought together.

#### PTEROSAURS.

The *Dimorphodon*, till now the earliest-described long-tailed

Text-fig. 74.

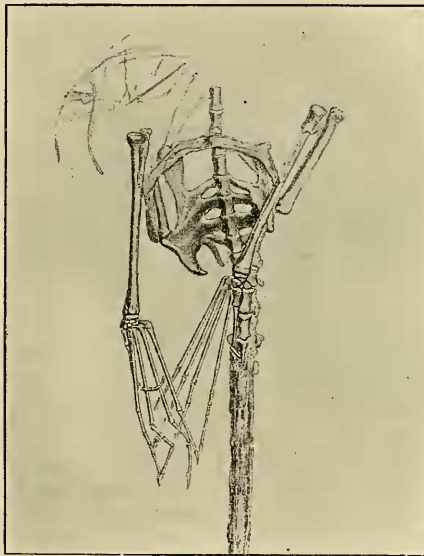


Hind limb of *Dimorphodon*

Pterosaur, shows in its hind limb no sign whatever of cursorial locomotion (text-fig. 74). The metatarsals 1-4 are equally developed,

but the 5th is somewhat thicker and also much shorter. The elongate phalanges of the 5th toe further prove clearly that no *cursorial* adaptation modified the form of these bones. Very much the same type of foot is visible in the equally long-tailed *Campylognathus*; and when we turn to the *Rhamphorhynchus* of the Solenhofen Slate (text-fig. 75), we find not only no cursorial modification of the four-toed slender foot but quite decided degeneration. However, according to Zittel, the number of phalanges in the 5th toe is perhaps somewhat greater than in the drawings given for *Dimorphodon* or *Campylognathus*. Since the spur-like clawless 5th digit of the foot is very strongly developed in *Dimorphodon*, there is, as Owen observed, good reason to believe that a

Text-fig. 75.

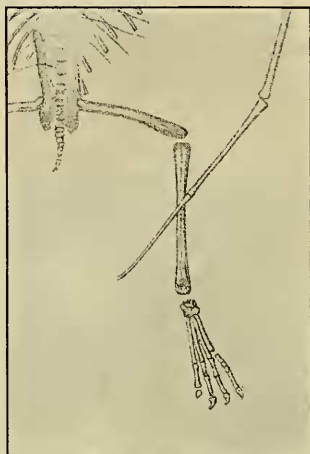
Hind limbs of *Rhamphorhynchus*.

uropatagium was not only present but even very well developed; whereas we know that in *Rhamphorhynchus*, in accordance with the less developed 5th toe, no uropatagium extended to this part of the body. The resemblance of the *Rhamphorhynchus* sternum to that of the Bat (*Taphozous*) likewise has to be noticed.

That in the Liassic *Dimorphodon* the wing-finger is relatively shorter than in the Tithonian *Rhamphorhynchus* is a fact so obvious as scarcely to demand attention. The short-tailed Pterosauria of the genus *Pterodactylus*, with comparatively short wing-bones, resemble *Campylognathus* in having four feeble and

equally strong metatarsals which all approximately attain the same length, while, in harmony with the lack of a tail, of the 5th toe only a rudiment (text-fig. 76) now remains. Among Chiroptera we find that in the tailless forms, notably *Pteropus*, quite similarly the os calcar of the hind leg is less developed than in the long-tailed species.

Text-fig. 76.

Hind limb of *Pterodactylus*.

(The rudiment of the 5th toe is unfortunately not shown in this drawing.)

On account of the anterior prolongation of the ilium in Pterosaurs, and on account of the great number of vertebræ united in the sacrum, it has been frequently assumed that the Pterosaurs enjoyed a bipedal locomotion. Both these arguments, however, fail to convince me, and this principally on account of *Nyctosaurus*, which, although certainly not a bipedal genus, has a still greater number of sacral vertebræ, and because in *Pteropus* there is likewise a pseudosacrum present. Another argument that can be brought forward as annulling the hypothesis just mentioned consists in the fact that the Pterosaur pelvis, though showing considerable length, has an ilium of an exceedingly low and narrow *Bat-like* outline.

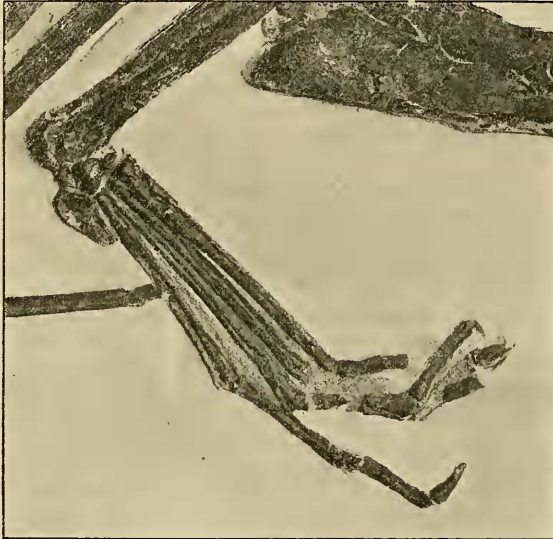
A Pterosaur of whose crawling habits we can be quite sure is, as just mentioned, the Upper Cretaceous *Nyctodactylus*, for, as Williston pointed out, the acetabulum is placed far back, nearly over the edge of the sacrum, so that it was impossible for the knees in this animal to meet in the middle, and at times the knees may even have been turned outward and less backward. When the femora were rotated outward and abducted, the tibiæ might have been brought parallel with each other. Exactly similar conditions are

to be met with among Bats, whose crawling locomotion is familiar to every student.

The elongation and attenuation of the hind feet in *Nyctodactylus* (text-fig. 77) are also characters that demand mention, and a similar elongation is again to be met with in the tailless Vampires.

An interesting feature is the co-ossification of numerous dorsals in *Nyctodactylus* and the nearly allied European genus *Ornithocheirus*.

Text-fig. 77.



Hind limb of *Nyctodactylus*.

(Photograph of specimen in the British Museum.)

A Triassic long-tailed Pterosaurian, *Tribelesodon* (the detailed description of which I intend publishing on some other occasion), shows much the same proportion between total length of hind and fore limbs as does *Galeopithecus*; and, although *Galeopithecus* proves to be in no way related to Chiroptera, still we must suppose that the whole order Chiroptera, considering the patagium, passed through a *Pteromys*- and a *Galeopithecus*-like stage in the course of its evolution.

Since, as already pointed out, a patagium requires many spear-like supports, and since in arboreal animals fore and hind limbs are to the same extent used for running and leaping, it is evident that primarily fore and hind limbs must have become to the same extent used for the support of the patagium, which necessarily had to take origin at the centre of gravity between humerus and femur.

As soon as such a potentially flying animal became actively

volant, and began to fly by force—that is, move its patagium, —the sternum must evidently have developed a sternal crest, the patagium must have continued to increase its surface, and this then would not only produce stretching of the limbs but also development of secondary supports of the patagium.

Such secondary supports are, as we shall see, developed at different times and in different ways, being produced by special development of the olecranon, the carpal bones, and ossified tendons. In the long-tailed Pterosaurs such supports are absent in the fore limb; in the short-tailed Pterosaurs, however, they are well developed and are represented by a modified carpal which, according to Williston, shows (*Pterodactylus*—*Nyctodactylus*) progressive evolution. Another modification that each patagium produces in the animal's body is to bring all the radial supports to the same level, and this, making the acetabulum and knee rotate outward and backward, produces subsequently crawling locomotion.

When the last stage of development is attained and aerial locomotion accomplished by skill and not by force (*Nyctodactylus*, *Rhamphorhynchus*), the patagium obviously not only would assume a pointed outline and become reduced to a smaller surface, but in some cases also the tail would change to a rudder-like organ (*Rhamphorhynchus*) or become entirely lost, while the attenuated feet would in this case assume the function of steering (*Nyctosaurus*). It is of no small importance that of the two highly specialised groups of Pterosaurians (*Rhamphorhynchidae* and *Nyctosauridae*) the tailless ones should have survived the longer.

#### MAMMALS.

Very much the same changes as are to be found between *Tribesodon*, *Dimorphodon*, and *Rhamphorhynchus* on the one hand, and *Pterodactylus* and *Nyctodactylus* on the other, are also to be observed when we come to consider the patagium-flying Mammals. A set of good diagrams of flying mammals has recently been published by R. S. Lull. *Petaurus* and all other animals with a small patagium represent the stage where, as in all arboreal animals, a very long tail is present.

Only a plagiopatagium is present in *Petaurus*, a propatagium is added in *Pteromys*, whilst in *Anomalurus* even a uropatagium is present. As in Pterosaurs, supplementary patagial supports are frequently developed. In *Anomalurus* and *Vespertilio* such a support arises from the olecranon, in *Pteromys* it is partially attached to the pisiforme and partially, though to a less extent, to the 5th metacarpal; and in embryos of Chiroptera quite a similar structure is met with: a modification recalling the backwardly directed toe of the hind leg in *Dimorphodon* is produced by the development of the calcaneum's calcar projection. As in Pterosaurs, so also in flying Mammals a very low ilium is present, and this not only in Chiroptera but also in *Galeopithecus*, where,

even during ontogenetical evolution, a backward rotation of the ischium, and in consequence a flattening of the pelvic girdle, is to be met with. *Pteromys* and *Anomalurus*, according to Dollo, have to be termed passive flyers: the first partially active flyer seems to be *Galeopithecus*, for, according to Wallace, this animal is not only capable of sailing downward, but at the end of its downward oblique glide to rise a little upward.

*Galeopithecus*, however, is a long-tailed, comparatively short-armed patagial animal, in which nevertheless the patagium extends even to the tips of the digits and to the end of the tail; while when we turn from this to the specialised actively flying Chiroptera, we are impressed firstly by the elongation of the wing, and secondly by the frequent partial or total loss of the tail.

Both in Pterosaurs and Bats the main movement during flight seems to have been, and still is, dependent on the humeral articulation. The similarity of the patagial structure in *Rhamphorhynchus* and Bats, as remarked by Zittel, is also to be noted. The hairless condition of the patagium in Chiroptera compared with *Galeopithecus* is likewise a more specialised feature; while *Pteropus vulgaris* (more specialised than any Bat in regard to the caudal region, "chevauchement de spécialisation") shows, by possessing some hair on the interior surface of the patagial membrane, an intermediate stage.

In Pterosaurs, as also in *Pteropus*, the number of sacrals is augmented, and in the latter they even form, by co-ossifying with the ischium, a pseudosacrum.

The more or less perfect reduction of tibia and ulna is another character that is noteworthy in all patagium-bearing Mammals.

In an analogous manner to the Cretaceous *Ornithocheirus*, also in some Bats a rigid thorax is attained, though in this case the ribs and not the vertebræ co-ossify.

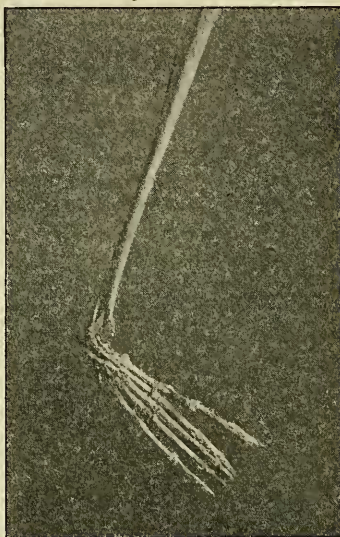
Since we may safely assume that Bats descended from Mammals which possessed a well-developed neural spine, the reduction of this process, noticeable also in the Flying Lizard (*Draco volans*), has also to be considered as a sign of specialisation.

The thin and dense skull-bones also unite in specialised Bats, very much as in Birds and Pterosaurs; and as to the brain, there exists a great amount of resemblance between the cast of the brain-cavity in some Eocene Bats, in *Hesperornis*, and in *Scaphognathus*.

Only in one point is there a pronounced difference between the Pterosaurs and the Bats, and this is in the transformation of the phalanges of the pes and manus. While in the Pterosaurs a reduction of the claws takes place in the pes, and they remain present in the manus, in Chiroptera exactly the opposite happens; but this divergence is easily understood when we consider that the Chiroptera had, in consequence of adapting four fingers to flight, only their hind feet at their disposition, for resting and suspending on branches, while the Pterosaurs, which developed only one

wing-finger, could always suspend themselves by the remaining free digits. This is, perhaps, also the reason why, in both groups, ulna and radius, tibia and fibula have been reduced in a different manner. In Birds the same problem has been solved in quite another manner (musculus ambiens and peculiarities in the structure of the tendon-sheath of musc. flexor. digit. in the phalanges). Text-fig. 78 shows the hind limb of a Bat identified by Dr. K. Andersen as *Hipposiderus gigas*.

Text-fig. 78.

Hind limb of *Hipposiderus*.

Since all flying animals must needs have developed from agile quick-moving animals, since all living patagium-flying animals (such as *Draco volans*, and the other living animals mentioned in this paper) are arboreal, leaping, quadrupedal creatures, and since, further, a bipedal cursorial animal, on account of mechanical impossibilities, can never develop a patagium—for such an organ would in bipedal (*i. e.*, erect) locomotion only catch the air and so prevent running without raising the body,—and since the union of fore and hind limbs is directly opposed to bipedal cursorial locomotion, we can safely state that all patagium-flying animals originated from quadrupedal, leaping, arboreal forms.

Bats and Pterosaurs, though they support the wing in different ways, still show an analogous direction of evolution—as shown by the development of a patagium with all that this implies; thus we may safely state that *Bats and Pterosaurs have arisen in similar manner from quadrupedal arboreal forms.*



## DINOSAURS.

In consequence of the quite extraordinary tendency of Dinosaurs to specialise every now and then along Avian lines, and in consequence of the fact that the most primitive Dinosaurs are bipedal in their habits, it is not only probable that all Dinosaurs originated from bipedal forms (I only need to quote the numerous bipedal tracks in the Red Triassic Sandstone in Connecticut), but that they also are very nearly related to the primitive Birds.

Since Dr. Holland thinks that the Dinosaur likeness to Birds is sometimes greatly exaggerated, I would like to mention some of the most characteristic primitive and adaptive Avian features of Dinosaurian reptiles: basis cranii (*Hypsilophodon*, *Compsognathus*), development of beak (Orthopoda, beak perhaps developed independently in different suborders, caused by latent homoplasy), lack of neural spines in cervical vertebræ (Sauropoda), dorsal neural spines bifid (*Diplodocus*), saddle-shaped articulating surface of sacrales (*Streptospondylus*), synsacrum (Orthopoda), *Æpyornis*-like caudals (*Diplodocus*), Avian scapula (Orthopoda, Theropoda), co-ossification with the coracoid (all Dinosaurs), manus (*Ornitholestes*), ilium covering last ribs (Sauropoda), ilium touching neural spines (Stegosauridæ), ilium showing antitrochanteric ridge and dorsal plane (Theropoda); backward rotation of pubis and subsequent development of processus pseudopectinealis (Orthopoda), femur shorter than tibia (many Dinosaurs); reduction of fourth trochanter (all Dinosaurs), distal end of femur (*Streptospondylus*, &c.), development of processus ascendens astragali (Theropoda), fusion of calcaneum and astragalus with tibia (*Compsognathus*); position of hallux (Theropoda); pneumaticity or light structure of the whole skeleton (many Dinosaurs).

In a paper on the evolution of Dinosaurs, I pointed out that the Theropoda specialise by developing an interpubic ossification, by augmenting the number of their sacrales, by changing the character of their vertebræ from biconcave to opisthocœlous, by lengthening their neural spines in the dorsal region, and by developing a proc. asc. astrag. and reducing the number of their toes. In more specialised Theropoda the metatarsals become always more closely applied, and, lastly, these animals specialise by losing the fourth trochanter. Most of these changes are also notable among the bipedal Orthopoda, and since this development is independent of that in the Theropoda, we must consider them as homodynamic changes; besides this, in Orthopoda we can trace a thickening of the bony matter and the development of a processus pseudopectinealis. A functionally analogous osseous process is developed in most running birds after the co-ossification of the pelvic elements.

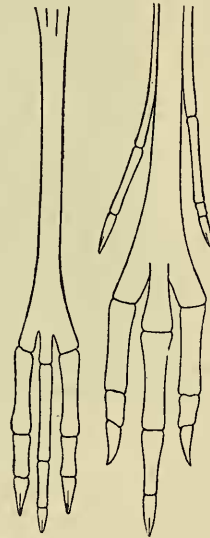
Since we can be sure that in Dinosaurs all the changes mentioned are not due to the giving up of volant habits, but are merely signs of cursorial adaptation, we have a clue to understand some of the changes that occur among the Palæognathous Birds. Besides this we can fix the fact that the Dinosaurs, like

many cursorial Mammals, were not only set the problem of developing a flexible dorsal vertebral column, which was attained by development of convexo-concave intervertebral articulation, but that to this, in consequence of the position of their head, they had to add strength in the vertical direction, which could only be attained by developing the attachment surfaces for the musculus longissimus dorsi on the neural spines and the producing of hypapophysis-like knobs on the cervicals. This, moreover, is the first consideration adduced since 1887 that shows us that the vertebral column of *Iguanodon*, though provided with ossified tendons, cannot have been altogether rigid. Text-fig. 79 is intended to show the highly modified foot of the Cretaceous Dinosaur *Ornithomimus*, and can be compared with the feet of *Dipus* and *Alactaga* (text-fig. 80).

Text-fig. 79.



Text-fig. 80.

Text-fig. 79.—Hind limb of *Ornithomimus*.80.—Hind limbs of *Dipus* (left) and *Alactaga* (right)

#### BIRDS.

Leaving Dinosaurs and turning to Birds, we observe the following salient points:—

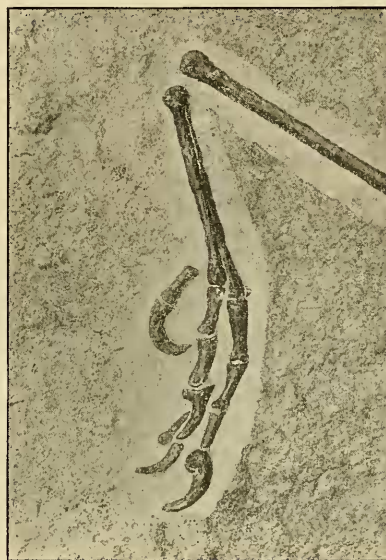
The first and most primitive Bird we know, *Archaeopteryx* (text-fig. 81), shows not only a perfectly bird-like femur and tibia, but also tridactylism, and this is, as demonstrated by Dinosaurs and the *Dipus*-like rodents, a prominent feature of bipedal cursorial or saltatorial specialisation, while it never occurs among arboreal forms.

The pelvis of *Archaeopteryx*, moreover, is essentially that of a Bird,

and as a sign of cursorial locomotion there is even an indication of a *processus pectinealis*. The vertebræ are free, and neural spines are present.

Besides this, *Archæopteryx* differs from all Birds by having a long laterally feathered tail, that to a certain degree reminds us of the peculiarly covered and flat-looking tails in the mammals *Acrobates* and *Ptilocercus lowi*.

Text-fig. 81.

Hind limb of *Archæopteryx*.

(Photograph of the British Museum type specimen.)

The ossified tendons which occur in the tail of *Archæopteryx* show further that strength of this organ was required just as much as in the tail of *Dimorphodon* or *Rhamphorhynchus*. A long tail, sometimes even with ossified tendons, is quite a marked feature of the Dinosaurian bipedal reptiles, and its loss, as shown in Pterosaurs, is generally in harmony with the better adaptation to flying locomotion.

The rounded contour of the *Archæopteryx*-wing, together with the feebly developed sternum, show us that *Archæopteryx*, though perhaps not an altogether badly flying creature, can on no account have been a soaring bird, but a bird that was yet in the first stage of active flight.

That the soaring Frigate-Birds and Albatrosses have a comparatively weaker sternum than the Gallinaceous Birds has already been mentioned; and I therefore need only point to the formation of a rigid thorax in flying birds as analogous to the condition in Pterosaurians and Bats and in opposition to the Ratitæ, and to the fact that the cursorial Palæognathæ, contrary to the flying

Tinamous, possessed not only free vertebræ, but even elongate, Dinosaurian-like neural spines in the dorsal region, and this because also in this case, for running, strength had to be united with mobility in the dorsal region, whereas for flight, as already mentioned, strength and rigidity seem to be the qualities required, so that the neural spines become to a certain extent useless. It is especially to the curious dorsal and caudal vertebræ of *Epyornis* that I should like to draw attention. Probably mobility is one of the reasons why in the flightless *Hesperornis* saddle-shaped vertebræ were developed at a period when *Ichthyornis* still showed biconcave articulation, although I am quite aware that perhaps other explanations will have to be sought for, since also in other ways *Hesperornis* indicates a more specialised form, and this not only by its wing-bones being already reduced, but by exhibiting a certain tendency to lose its teeth, since these are no longer placed in distinct sockets as in *Archæopteryx* and *Ichthyornis*, but in a furrow.

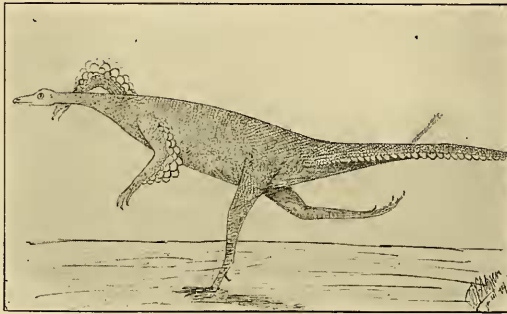
If we, after these preliminaries, now suppose that Birds, before attaining the *Archæopteryx*-state, originated from quadrupedal arboreal animals and only after having learnt to fly became bipedal, it is difficult to understand why they in general show Dinosaurian affinities, why they did not use both hind and fore limbs to the same extent for flight as they would have done for arboreal locomotion, why the bones of the pectoral region and of the wings show more primitive traces than the hind parts of the body, and why they did not, like all other quadrupedal flying animals, develop a patagium; whereas, if we consider that in *Archæopteryx* the anterior extremities, though bearing the most important ectodermal pinions, are less modified than the posterior extremities, which are already perfectly bird-like, and if we then suppose that Birds originated from bipedal Dinosaur-like Reptiles, it is easy to understand what induced the Birds to attain an *Archæopteryx*-like stage of evolution, for at first a certain amount of bipedal, and only afterwards a volant, modification would be required.

While we can safely state that a bipedal animal never could or did develop a patagium without giving up bipedalism, this cannot be said of feather-bearing forms, for we may quite well suppose that *birds originated from bipedal long-tailed cursorial reptiles which during running oared along in the air by flapping their free anterior extremities*. If Dinosaurs had bird-like pulmonary appendages, as indicated by the pneumaticity of the skeleton, such movement would only have been of advantage for the respiratory organs (the pneumatic foramen occurring sometimes in Moa-bones would therefore be an atavistic feature, and the loss of pneumaticity would be a parallel to the same change in the Dinosaurian subclass). At this point the pulmonary appendages of Chameleons have also to be taken into consideration. A double running and flapping action would—somewhat in accordance with Pycraft's views on this subject—subsequently easily lead to an enlargement of the posterior marginal scales of the antibrachium, and at the same time produce a certain amount of bipedal specialisation.

By gradually increasing in size, the enlarged but perhaps still horny hypothetical scales of the antibrachial margin would

in time enable the yet carnivorous and cursorial ancestor of Birds to take long strides or leaps, much in the manner of a domesticated Goose or of a Stork when starting, and ultimately develop to actual feathers; this epidermic cover would also raise the temperature of the body, and thus help to increase the mental and bodily activity of these rapacious forms. The possibility of such a development of flight is clearly shown by the somewhat analogous, but still more marvellous and nearly paradoxical, yet not unfrequent, development of Flying-Fishes. The marginal scales being originally the principal wing-element in such a hypothetical form, these parts could attain quite a considerable size without essentially altering the underlying bones of the arm, a fusion of the carpal phalanges being only then necessary, when in flight rigidity of this region became requisite. Besides this, the continued use of the anterior flapping limbs as

Text-fig. 82.



Hypothetical reconstruction of a running "Pro-Avis."

grasping-organs would also account for the feeble specialisation of the digits in the *Ornitholestes*-like manus of *Archaeopteryx*, and for the preservation of the claws in the Ostrich and *Opisthocomus*, where, according to Pycraft, the temporary delay in the growth of the distal pinions has been developed simply not to prevent the claws from performing their still not unimportant function. An effort to condense these hypothetical changes into a drawing is given in text-fig. 82, which might in consequent allusion to Pycraft's analogous reconstruction be called a "Pro-Avis."

The facts that even from the Eocene formation in most parts of the world numerous big Ratites are known, which can only have originated from badly-flying ground-birds, whereas in more modern times the Ratites are apparently vanishing from the earth's surface, likewise find quite an easy explanation in the hypothesis that in the Mesozoic times badly-flying ground-birds, and *not* tree-birds, were the prevailing forms. The individual or ontogenetical development of every cursorial Carinate (for example, every gallinaceous bird) would thus show us the exact manner in which flight has been acquired. The true phylogenetic value of the surviving "Palaeognathæ," with their body-temperature

decidedly lower than in other birds on the one hand (Sutherland), and their reduced brachioisternal muscles on the other (Fürbringer), can likewise be appreciated only if we consider them as forms that specialised at a very early stage of Avian evolution.

It is to be remarked that among the terrestrial birds which according to this hypothesis would seem to have preserved their original mode of living and manner of breeding, the nest-building faculty is less developed than in those birds which, to avoid the dangers of ground-life, migrated up into the trees and had then to shelter their eggs and young ones from the new chance of falling to the ground. That ground-life involves for a bird more dangers than life on a tree, I think, is shown by the fact that the true ground-birds usually are protectively coloured, while in the latter, even among Gallinaceous Birds, bright—one might nearly say artistic—sexual characters are frequently developed.

The supposition, that Birds once possessed a patagium and only afterwards developed feathers, I consider as devoid of foundation, for apart from the impossibility of a marginal feather being effective, when only attached to a flexible membrane, it is loss and not development of hair and scales (= epidermal coverings) that takes place in the Chiropterygian and Pterosaurian patagium. Besides, I do not see any reason why a useful patagium, once developed, should suddenly have stopped growing.

The long tail in *Archaeopteryx* can in no way be invoked in favour of a primitive arboreal stage of Birds, for a long tail not only characterises arboreal but also bipedal cursorial and saltatorial forms. Thus we cannot find a single character in *Archaeopteryx* that would absolutely prove arboreal specialisation, while the development of the cannon-bone alone is sufficient to show with certainty that some of the direct ancestors of *Archaeopteryx* had cursorial habits.

#### CONCLUSION.

From a consideration of the whole of the above remarks, we can, I believe, formulate the following statement:—

*While Pterosaurs and Bats originated independently from quadrupedal arboreal forms in which both anterior and posterior extremities, in consequence of the development of a patagium, became primarily equally used for flight and in consequence equally unfit for locomotion on the ground, Birds originated from bipedal Dinosaur-like running forms in which the anterior extremities, on account of flapping movements, gradually turned to wings without thereby affecting terrestrial locomotion. This is also the reason why Birds became dominant over all the rest of their aerial rivals.*

In conclusion, I take pleasure in thanking once more all the gentlemen that helped me to compile this paper, notably Dr. K. Andersen, Mr. G. A. Boulenger, Dr. Forsyth Major, Mr. W. P. Pycraft, and Dr. A. S. Woodward, at the British Museum of Natural History.